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ADDITION TO KNOWLEDGE OF GROEBERIA (MAMMALIA, MARSUPIALIA) FROM THE MID-CENOZOIC OF ARGENTINA

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ABSTRACT. *Groeberia pattersoni*, new species, from the Divisadero Largo formation, is based on the second known specimen of that genus. Some information on the hitherto unknown skull of genus and family is provided. Reference to the Marsupialia is supported, but affinities within the Marsupialia remain dubious.

The extraordinary fossil marsupial genus *Groeberia* has hitherto been known from a single specimen, a fragmentary mandible, named and described by Patterson (1952). A second specimen was found by Dr. Edgardo Rolleri of the Yacimientos Petrolíferos Fiscales (Argentine government petroleum bureau) and deposited in 1968 in the Museo de La Plata. Dr. Rosendo Pascual kindly referred it to me for study, which I carried out in La Plata early in 1970, and for publication, here presented. Sr. Jorge Zetti, assistant to Dr. Pascual, facilitated the study and arranged for photographs, provided by the Museo for this publication. The accompanying drawings were made by RaVae Marsh on the basis of sketches by me. I am also indebted to Dr. A. J. Amos, Dean of the Faculty of Natural Sciences and the Museum of La Plata, and to Sr. G. J. Scaglia, Director of the Museo Municipal de Ciencias Naturales of Mar del Plata, who sent the holotype of *G. minoprioi* on loan to La Plata for direct comparison with the present specimen.

The research for this paper was performed while I was employed jointly by the University of Arizona and the Museum of Comparative Zoology.

Class Mammalia Linnaeus, 1758
 Order Marsupialia Illiger, 1811
 Family Groeberiidae Patterson, 1952
 Genus *Groeberia* Patterson, 1952
Groeberia pattersoni, new species

Etymology. For Bryan Patterson, who named and described the genus and its type-species, *G. minoprioi*.

Holotype. Museo de La Plata No. 68-VI-27-1, partial skull and mandible.

Hypodigm. Holotype only.

Horizon and locality. Divisadero Largo formation, [in the general vicinity of] Mina Atalá, Mendoza, Argentina.

Diagnosis. Anterosuperior part of symphysis much more slender and incisors smaller than in *G. minoprioi*. M_{3-4} also, but less, smaller. See Table 1.

Identification. The holotype of the type-species *Groeberia minoprioi* includes most of the mandibular symphysis and incisors, left M_{2-3} , and broken bases of M_1 and M_2 (see Patterson, 1952). The present specimen also preserves most of the symphysis and lower incisors and has the broken bases of left M_{3-4} . These parts are morphologically closely similar in the two specimens and quite unlike any other animal known to me. Reference to the same genus is indicated. Both are from the Divisadero Largo formation and

TABLE 1

Comparative measurements in millimeters of holotypes of
Groeberia minoprioi and *G. pattersoni*.

	<i>G. minoprioi</i>	<i>G. pattersoni</i>
Transverse at narrowest part of symphysis, at postincisive diastema	ca. 5.8	ca. 3.4
Transverse, across both incisors at alveoli	ca. 5.8	ca. 3.4
M_3 Length	2.3	ca. 1.8
M_3 Width	1.6	ca. 1.4
M_4 Length	ca. 2.3	ca. 1.5
M_4 Width	ca. 1.8	ca. 1.3

Measurements of M_3 of *G. pattersoni* and of M_4 of both specimens are on broken bases of teeth and are rough approximations.

near the same locality: the holotype of *G. minoprioi* from one-half kilometer east of the Cerro Divisadero Largo (Patterson, 1952: 3) and that of *G. pattersoni* recorded as "Mina Atalá," which would be about 1¼ kilometers northeast of the previous locality but which must be a rough approximation, as the Mina Atalá is not on the Divisadero Largo formation.

The holotype of *G. minoprioi* is from Minoprio's stratum F (see map and stratigraphic discussion in Simpson, Minoprio, and Patterson, 1962). The level of the present specimen is not so precisely known. Although no faunal change has been demonstrated within the formation, its deposition may have covered a considerable span of time and the two specimens may not be very closely contemporaneous. There is some presumption that specimens so similar in morphology and provenience are conspecific, but, as far as I know, the difference in slenderness of the symphysis and sizes of the teeth are greater than within adults of any one species of marsupials. This difference can hardly be due to greater age of the holotype of *G. minoprioi*. The incisors of the holotype of *G. pattersoni* do not taper in the alveoli, hence they could age considerably without increasing in diameter at the alveoli. Although measurements are imprecise, the length of M_1 is about 50 per cent longer in the holotype of *G. minoprioi*, and these brachydont teeth do not grow after eruption. The holotype of *G. pattersoni* evidently had all teeth erupted and some skull sutures closed, as in fully adult animals. Thus specific separation is indicated.

Age. Simpson, Minoprio, and Patterson (1962: 290) concluded that "the age of the Divisadero Largo fauna is approximately early Deseadan or latest pre-Deseadan," but that knowledge at that time did not warrant basing on it the apparently missing mammalian age-stage between Mustersan and Deseadan. However, on evidence not fully stated, Pascual, Ortega, Gondar, and Tonni (1965) proposed a "Divisaderense" (in English, Divisaderan) mammal age-stage as intermediate between Mustersan and Deseadan and separated from each by a hiatus. They tentatively correlated it with the Ludian of Europe and Duchesnian of North America as latest Eocene. As those authors also did recognize, the data do not really permit close correlation, and I believe that all one can now say is that the age in terms of the European epochs may be somewhere around late Eocene or early Oligocene, hence, in terms of absolute age, more or less middle Cenozoic.

Description. As found, the specimen included at least the anterior part of the skull and most of the mandible in articulation. Some time before the specimen came into the control of the Museo de La Plata, the skull and mandible were separated and both were severely damaged. Nevertheless, what remains adds considerably to knowledge of this remarkable and enigmatic genus.

The two lower incisors are preserved for a length of about 12 mm within their alveoli. The anterior ends are broken and the posterior ends have been ground smooth, presenting the appearance seen in Figure 1B. The pulp cavity is here open, and there is no sign of root formation, so these teeth were clearly hypselodont,¹ as in *G. minoprioi*. The teeth curve so that the posterior parts were nearly horizontal, in an odd medial posterior projection of the symphysis, and the extra-alveolar parts would have been nearly vertical. Enamel is lacking on the medial and dorsal faces, and at this depth in the alveoli even the dentine has not quite closed the pulp cavity dorsally. Heavy enamel occurs ventrally, and this extends, thinning as it goes, onto the lateral faces, more so than in the extra-alveolar parts of the incisors of the holotype of *G. minoprioi*.

There is a short diastema posterior to the lower incisors and then a series of cheek teeth, probably four as in *G. minoprioi*, although here they cannot be definitely counted. The bases of what are almost certainly the last two cheek teeth can be made out, but the crowns are not visible. These teeth are brachydont as in *G. minoprioi* and similar in outline but perhaps slightly less elongate.

There are two pairs of upper incisors, here designated I¹ and I² for convenience, although their ancestral homologies are unknown.

¹ Dictionaries give "hypselodont" as a variant of "hypsodont," and the most recent authoritative odontology, Peyer (1968), uses "hypselodont" in place of "hypsodont." It is, however, more convenient to adopt a distinction sometimes made by mammalogists, especially paleomammalogists. I define as *hypsodont* a tooth that eventually develops one or more roots but that has a crown definitely higher than those roots or than any of its horizontal dimensions and, as *hypselodont*, a tooth that never forms a root but continues to grow and to extrude new parts from the alveolus throughout life. Peyer was not a mammalogist and devoted relatively little attention to mammal teeth. Other odontologists have often oriented their work on groups, especially *Homo*, in which hypselodont teeth (in my sense) do not occur. The distinction is of great functional importance.

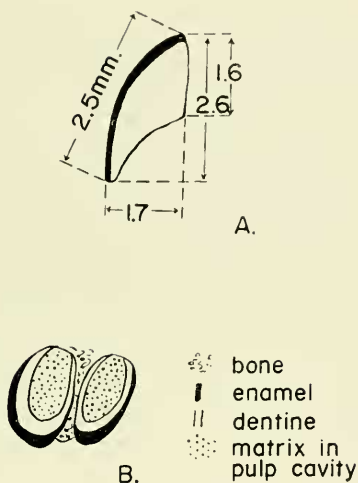


Figure 1. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. A. sketch and measurements of wear surface of I¹, approximately $\times 6$. B. sketch of posterior (intra-alveolar) exposure of paired lower incisors, approximately $\times 5$.

I¹ is a large, strongly curved tooth with an alveolus extending posterodorsally far back in the facial region to above the infra-orbital foramen. It and I² are probably both hypselodont. The cross section is peculiar, with an oblique, long, slightly convex, buccal, enamel-covered face; a flat, anteroposterior, enamelless, anteromedial face; and a likewise enamelless, concave, posteromedial face. The three faces meet at definite angles, approximately right angles at both ends of the anteromedial face but strongly acute between the buccal and posteromedial faces. (See Fig. 1A.) The enamel is nearly smooth but with slight wavy longitudinal ribbing. Right and left I¹ are close to each other on their medial faces.

I² is much smaller than I¹, measuring about 1.1 mm across the buccal face as compared with about 2.5 mm for I¹. I² is also enameled on the buccal face, and probably not elsewhere. The cross section cannot be clearly determined as the specimen is preserved. I² is less curved longitudinally than I¹ and although

the extra-alveolar parts of the two are in contact, the alveoli diverge. In the most probable orientation of the skull, the extruded part of I^1 is slightly recumbent and that of I^2 is nearly vertical.

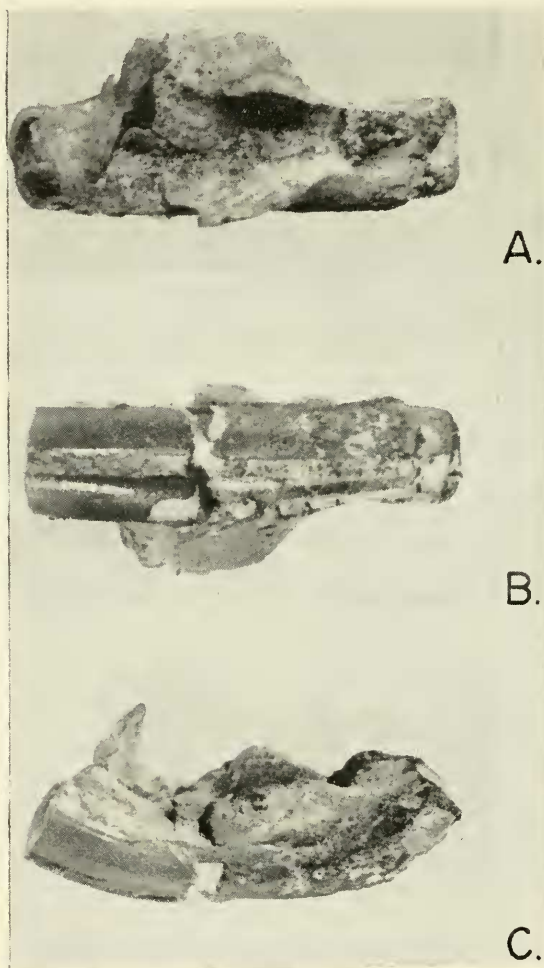


Figure 2. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. Fragment of symphysis with parts of lower incisors. A, supero-posterior or lingual view. B, infero-anterior or genial view. C, right lateral view (in more anatomical orientation the anterior parts of the incisors would be nearly vertical). Approximately $\times 4$.

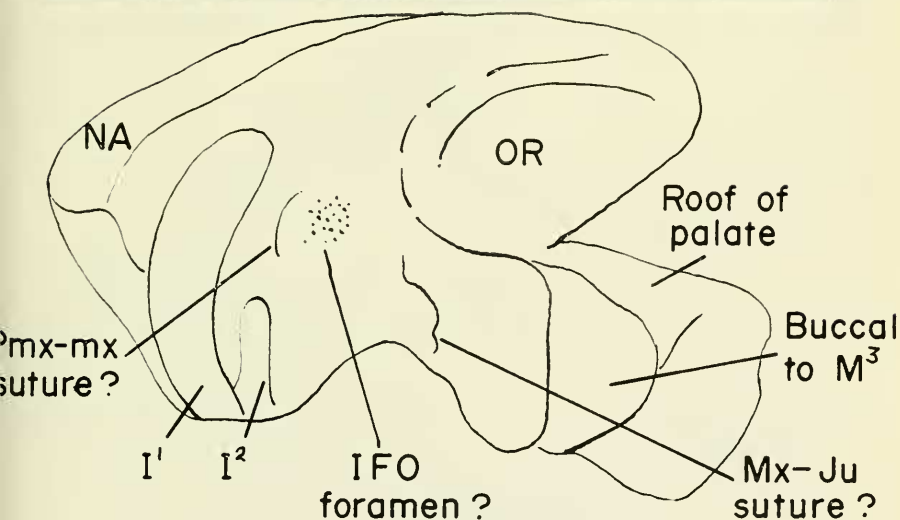


Figure 3. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. Anterior part of skull, left lateral view, photograph and explanatory sketch. "Buccal to M³" indicates a point on matrix, formerly covered by the zygoma, medial to which is a broken cheek tooth identified as probably M³. IFO = infraorbital. Mx-Ju = maxillo-jugal. NA = nasal. OR = orbit. Pmx-mx = premaxillo-maxillary. Approximately $\times 4$.

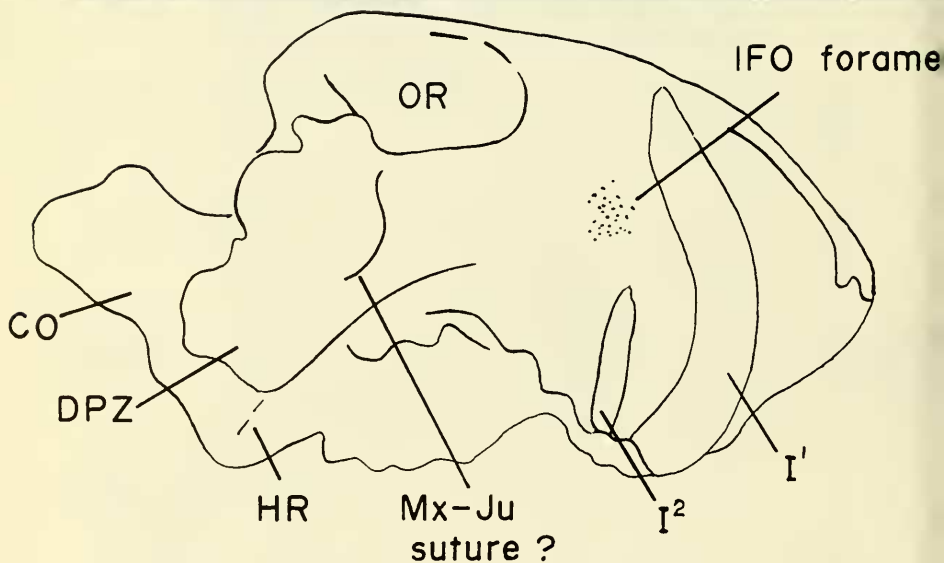


Figure 4. *Groeberia pattersoni*, new species. Holotype. M.L.P. No. 68-VI-27-1. Anterior part of skull, right lateral view, photograph and explanatory sketch. CO = fragment of coronoid process of mandible. DPZ = descending plate of zygoma. HR = fragment of horizontal ramus of mandible. IFO = infraorbital. Mx-Ju = maxillo-jugal. OR = orbit. Approximately $\times 4$.

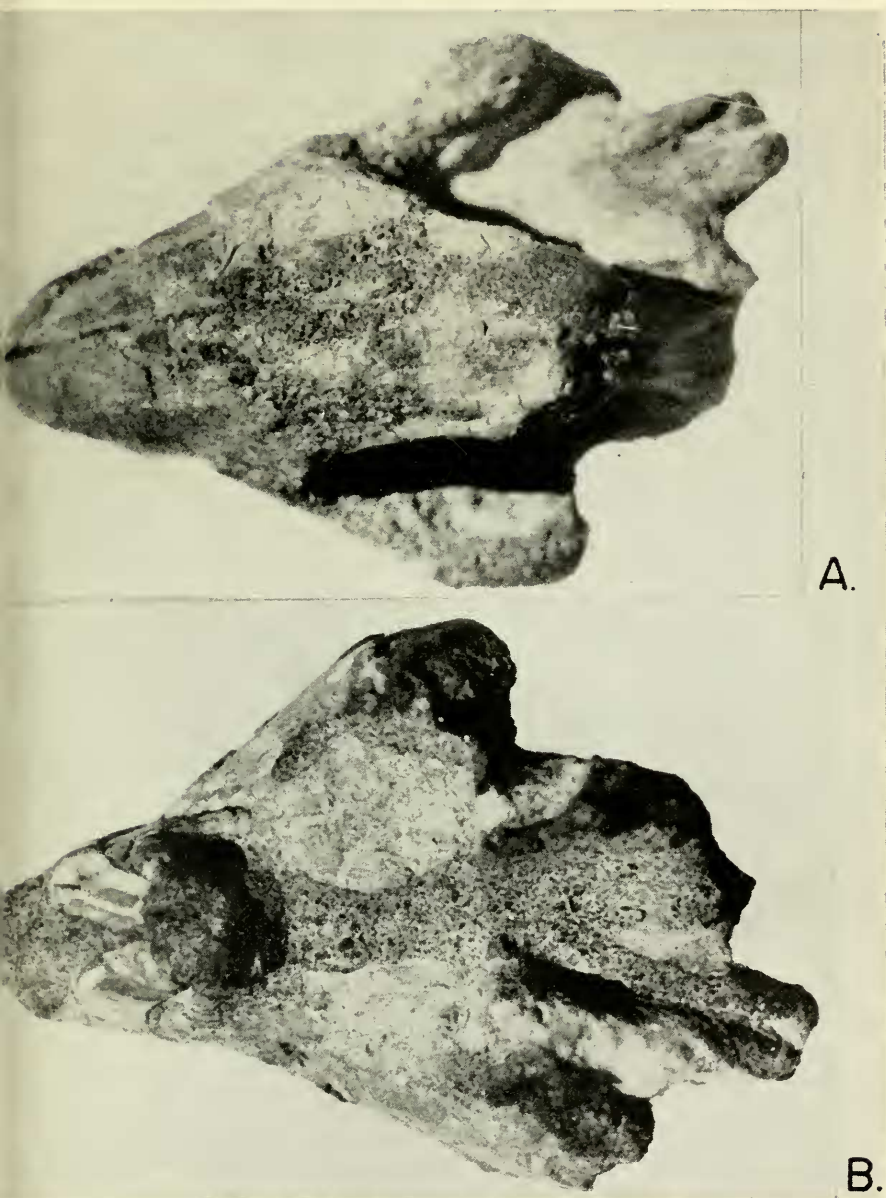


Figure 5. *Groeberia pattersoni*, new species. Holotype M.L.P. No. 68-VI-27-1. Anterior part of skull. A, dorsal view. B, palatal view. Approximately $\times 4$.

There is a diastema posterior to I^2 and then cheek teeth, but nothing definite can be made out for the latter, except that they are small and brachydont.

The preorbital part of the skull is notably short and deep. In the most probable orientation, it (or the snout) is convex dorsally as a whole and curves downward anteriorly. The nasals are accordingly downcurved and end shortly anterior to I^1 . The infra-orbital foramen is not definitely visible as the specimen is preserved, but must be of moderate size and in a normal position on the face anteroventral to the orbit and about half way between it and I^2 , where there is a depression obscured by matrix on the specimen. On the left side, what is probably part of the pre-maxillo-maxillary suture is visible just anterior to that depression.

The orbit is rather small and relatively anterior in position, its anterior rim probably in advance of the cheek teeth and certainly well in advance of what is identified as M^3 . The stout root of the zygoma below the orbit had an expanded suborbital process or plate, the full extent of which cannot be determined. On both sides, a possible but uncertain maxillo-jugal suture can be seen



Figure 6. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. Anterior part of skull, anterior view. Approximately $\times 4$.

below the ventral border of the orbit. Posterior to this, and hence on the jugal if the possible suture is such, is a small ventral postorbital process. Uncertainly but probably, there was no dorsal postorbital process, and the orbit was therefore probably open.

The palatal surface is both poorly exposed and poorly preserved, so that little can be made out there with sufficient probability. However, its dorsal (intranasal) surface is partly exposed, and some details can be made out in cross section at the broken posterior surface of the specimen. A palatal vacuity was probably absent or small if present. It appears that the palate between the cheek teeth was deeply arched (concave ventrally). The coronoid process of the mandible can be seen lateral to a posterior tooth, perhaps M^3 or M^4 , and lateral to that a section of a deep (vertically) but thin (laterally) zygoma. (See diagram, Fig. 7.)

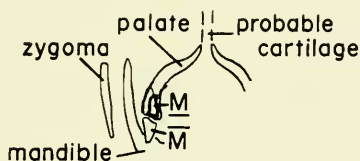


Figure 7. *Groeberia pattersoni*, new species. Holotype, M.L.P. No. 68-VI-27-1. Rough diagram of section at posterior break of specimen as preserved. Not to scale.

Affinities. This specimen adds considerably to data bearing on affinities of the genus, without settling the matter. Patterson's (1952: 3) judgment that *Groeberia* should be distinguished at the family level, as Groeberiidae, is strongly confirmed.

Patterson's evidence that *Groeberia* is a marsupial was in small part positive, largely negative, and partly indirect. The present specimen adds no positive evidence, strengthens the negative evidence, and does not change the indirect evidence. The only really positive evidence from the holotype of *G. minoprioi* for marsupial affinities in general (as distinct from caenolestoid affinities in particular, see below) is the probably inflected angle of the mandible. Even this is not quite certain, because the angle itself is not known, but a crest that would have led to it does decidedly suggest inflection. An inflected angle is strong, but not conclusive, evidence, as a few marsupials do not have the angle inflected and a few placentals do. *G. minoprioi* may have had four

lower molars, and that would again be strong but not fully conclusive evidence, but the possibility that its cheek teeth include one premolar and three molars is not entirely excluded. The known parts of the skull of *G. pattersoni* have no evident features strongly characteristic either of marsupials or of placentals. The absence of palatal vacuities would be more like most placentals, but it is uncertain and there are a number of marsupials without such vacuities.

The negative evidence is that *Groeberia* has no known features that would make reference to the Marsupialia impossible or highly improbable but does have known features that make reference to any other order highly improbable. Here the new specimen confirms and adds somewhat. The habitus is more or less rodent-like, but the two upper incisors are unlike those of any rodent. They are somewhat like those of lagomorphs, but the cheek teeth, even what little can be seen of them in this specimen, definitely rule out pertinence to that group. Limited resemblances of the mandible to those of certain primates, such as the early Cenozoic *Chiromyoides*, as mentioned by Patterson, or the living *Daubentonia*, become even less possibly significant in the light of what is now known of the skull. The skull is unknown in *Chiromyoides*, but its upper incisors are entirely unlike those now known in *Groeberia* and the skulls of other plesiadapids are also quite different (see especially Russell, 1964). There is an interesting resemblance between the short, deep faces of *Daubentonia* and *Groeberia*, but this is quite clearly functionally convergent and the two differ markedly in other respects and in facial details. Almost all other placental orders have basic diagnostic features absent in *Groeberia* or strongly contradicted in this genus.

If *Groeberia* was a placental, it must almost perforce have evolved independently and uniquely from ancestors as primitive and undifferentiated as those now known from the late Cretaceous and, in decreasing numbers and generality, quite early Cenozoic. Here one turns to the indirect and yet cogent evidence: that no such placentals are known from South America; that equally primitive and undifferentiated marsupials are known from there; that those marsupials did diverge in independent and unique lines; and that derivation of *Groeberia* from a potent and definitely South American source is at least a likely hypothesis.

Patterson's views on the affinities of *Groeberia* were buttressed by evidence for referring it to the Caenolestoidae. That evidence,

from the single poorly preserved fragment of mandible then known, was as follows:

1. One greatly enlarged lower incisor, with enamel on anterior face and alveolus (or "parte basal") parallel to median line of symphysis (not to the horizontal ramus or tooth row).
2. Strong salient coronoid process.
3. Molars with short talonids with posterior entoconid and hypoconid, united by a transverse crest, a short *crista obliqua*, and a shallow basin.
4. Molar trigonids with one lingual (probable metaconid) and two labial cusps (probable paraconid and protoconid), as in caenolestoids except Caenolestinae.
5. Trigonids and talonids subequal, as in Palaeothentinae and Abderitinae.
6. Masseteric crest absent; very poorly defined in Palaeothentinae.
7. Inflection of lower border beginning anterior to cheek teeth; usually posterior to cheek teeth in Caenolestoidea but beneath M_4 in *Parabderites bicrispatus*.

This was a valid analysis of the admittedly deficient evidence, but the conclusion may be retroactively queried in the light of present knowledge. As to (1), no unquestioned caenolestoids have hypselodont incisors comparable to these in form or function, but the placing of the alveoli is an interesting point. (2) is not particularly diagnostic. Regarding (3)–(5), the molar structure is difficult to make out on the specimen, but I believe that Patterson has correctly interpreted it. However, it differs characteristically from probably ancestral didelphid structure in little more than the more labial position of the paraconid, an occlusal adjustment that could well arise more than once. (6) is somewhat dubious and is not diagnostic for caenolestoids. (7) differs from caenolestoids more than it resembles them.

A reasonable but inconclusive case was presented on the basis then available and pending acquisition of further knowledge. The still quite limited further knowledge now acquired does not flatly contradict that case, but neither does it strengthen it, and it even weakens it to some extent. I see no special resemblance of known parts of *G. pattersoni* to any unquestionable caenolestoid. On the contrary, the extreme abbreviation of the face, the reduction of the incisors to two, and their truly gliriform, hypselodont nature

are almost the opposite of known trends in the Caenolestoidae. Even the Polydolopidae, superficially most seemingly rodentlike of undoubted caenolestoids, are not really very rodentlike in habitus and evolved in a direction very unlike that of *Groeberia* (see especially Simpson, 1948; Paula Couto, 1952).

Patterson (1952: 6) also compared *Groeberia* with *Argyrolagus* and concluded that they are not specially related beyond their both being marsupials. With greatly increased information on *Argyrolagus*, I agreed (Simpson, 1970), and the present addition to knowledge of *Groeberia* does not change that opinion. Indeed, the contrasts between *Argyrolagus* and *Groeberia*, both somewhat rodentlike, are remarkable. *Argyrolagus* has an extremely elongate, shallow rostrum and face, very posterior orbit, short, shallow zygoma, hypselodont cheek teeth. *Groeberia* has extremely short, deep rostrum and face, very anterior orbit, long deep zygoma, brachyodont cheek teeth.

Almost complete knowledge of dentition and skeleton of *Argyrolagus* contradicted previous opinion that it might be a caenolestoid and required placing it in a separate superfamily. I suspect that the same might happen if we had equally good information on *Groeberia*, but we do not. This knowledge is still so scanty that I believe it would be unreasonable or, at best, premature at this point to classify the Groeberiidae other than as *Marsupialia incertae sedis*.

Proposals have long been made to divide the marsupials into suborders, and recently, to divide them into two or more orders. If suborders Polydactyla and Syndactyla were recognized, I would predict that discovery of foot bones would align *Groeberia* with the polydactyls. If Polyprotodonta and Diprotodonta were recognized, *Groeberia* would be descriptively, typologically, or phenetically diprotodont, but I believe that would be profoundly misleading because it inevitably suggests connection with the Australian diprotodonts, and *Groeberia* is not so *incertae sedis* as all that. It has no suggestion at all of Australian affinities. The ordinal system of Ride (1964) has no sure ordinal place for it, as the evidence that it may be a "paucituberculate" (caenolestoid) is insufficient, but reference to the Marsupicarnivora would be rather anomalous (although like all marsupials it doubtless arose from the group so named by Ride), and pertinence to the Peramelina or Diprotodonta (*sensu* Ride) is out of the question. Kirsch's (1968) arrangement also has no sufficiently likely place for *Groeberia* in any one of his orders.

Biology. In the absence of postcranial remains, nothing can be safely inferred as to body build, limb proportions, or locomotion in *Groeberia*. Biological inferences are further limited by the absence of specimens of the neurocranium and by the imperfections of the only two specimens known. The following are the principal characters of probable functional importance that are known:

1. Face and snout short.
2. Face and mandible deep.
3. Infraorbital foramen small.
4. Orbit relatively anterior.
5. Orbit of moderate size.
6. Masseteric origin on zygoma.
7. Heavy hypselodont incisors with labial enamel.
8. I¹ recumbent.
9. Short lower diastema near alveolar level.
10. Comparatively small, brachydont cheek teeth.
11. Large coronoid process.
12. Small (no?) masseteric crest.
13. Inverted angle.

The habitus is rodentlike at first sight, but no living rodent and in fact no other animal, living or fossil, known to me combines all those characteristics. 3, 6, 11, and 13 are usual and 4, 5, and 10 common in marsupials; all but 13 are also fairly common in placentals. 1, 2, 7 and 8 occur in the other known marsupials that are most rodentlike, the Australian wombats. They are lacking in caenolestoids, also somewhat but much less rodentlike in some genera. With only the partial exception of 13, all these characters occur in one placental rodent or another, but not in this combination. For example some caviomorphs, such as *Echimys*, have characters 5, 7, 8, 10 and a functional modification of 13, but notably differ in 3, 6, 9, 11 and 12. *Aplodontia* has 3, 4, 6, 7, moderate 8, 11 and moderate 12, but differs markedly in 1, 2, 5, 9, 10, and 13. *Xerus* (a sciurid) agrees well in 1, 3, 4, 7, 8, and 10, but less well in 2 and 9, and not at all in 5, 6, 11, 12, and 13.

There is no doubt that *Groeberia* was a powerful gnawer, at least as much so as hares, rodents, wombats, or *Daubentonina*. Its incisors were not merely a pincer apparatus as in all known caenolestoids and all diprotodonts (phalangeroids) except the wombats. They are decidedly more adapted to gnawing than in the argyrolagoids, even though the latter, unlike caenolestoids, also have

hypsodont incisors. Gnawing is strongly connected with food gathering in recent animals, but not exclusively so. On the other hand, *Groeberia's* small area of brachydont cheek teeth is very different from the hypselodont teeth of wombats, argyrolagoids, and many rodents, and is more nearly comparable with the cheek dentition of caenolestoids, squirrels, and *Daubentonia*. The combination suggests a food obtained by gnawing but prepared for deglutition by crushing or comminution without grinding. Possibilities are bark or wood-boring insects or fruits or nuts with hard shells. However, some murids with strong gnawing apparatus and limited, brachydont cheek teeth are virtually omnivorous or even carnivorous. I see no way to correlate *Groeberia's* unique combination of characters with an equally unique diet or with any closely specific way of life.

No rodents are known in the Divisadero Largo or any earlier South American formation. Simpson, Minoprio, and Patterson (1962: 289) mentioned the possibility that the presence of the rodentlike marsupial *Groeberia* indicated age before rodents reached that area, hence pre-Deseadan. The ecological aspect of that suggestion would still hold even if the determination of the relative time of entry of rodents proved to be incorrect. (There is still no opposing evidence.) The rodent habitus surely evolved elsewhere and was in being when the first rodents entered South America, whether in the Deseadan or, as is quite likely, somewhat earlier. On the other hand, the ancestral habitus of *Groeberia* almost certainly evolved in South America before rodents reached there, convergent to some extent toward the absent rodents and entering niches with some points of similarity.

Zoogeography. It is the most reasonable hypothesis that the Groeberidae did evolve in South America, even though their possible relationship to the Caenolestoidae is quite dubious, and there is no suggestion of special descendant relationship (involving specialization) to any other South American group. Origin from South American didelphoids is as likely as any other, if not more so. There is no special resemblance to any Australian marsupials suggestive of genetic affinity beyond the remote ancestry of all marsupials. No marsupials are known from Africa and any idea of connection there would be purely gratuitous at present.

Nevertheless it is strange that three of the most peculiar, most specialized known groups of South American marsupials appear in the presently available record without known ancestors, only to

vanish again immediately (geologically speaking) or soon thereafter: Groeberiidae, only in the Divisadero Largo formation; Necrolestidae, only in the Santa Cruz formation; and Argyrolagidae, only from Huayquerian to Uquian. A possible clue is that all these faunas are in Temperate Zone Argentina and that earlier faunas are as yet very inadequately known farther north on the continent. It is a reasonable hypothesis, as yet without direct evidence, that these groups evolved in what are now (and quite likely were then) the tropics and are picked up in our record only when they spread rather briefly to what was for them a marginal area.

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